

Natural mortality ogives for the Indian Ocean bigeye and yellowfin tuna stock assessments

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Abstract

Natural mortality for bigeye tuna was estimated based on the maximum ages both in the Indian Ocean and in all oceans, using the method of Hamel and Cope (2022). Sensitivity to updated natural mortality (M) estimates was explored for the 2019 bigeye stock assessment. Sensitivity was similarly explored for the 2021 yellowfin stock assessment, based on M estimates from Hoyle et al (2023). The updated ogives for bigeye tuna tended to have higher M than the 2019 assessment for older fish, and consequently tended to increase the estimated productivity of the stock. In contrast, the updated yellowfin tuna ogives tended to have lower M than the 2021 yellowfin assessment for older fish, which implied lower stock productivity.

Further work is recommended in the following areas: 1) collect further data across all areas of the Indian Ocean for studies of age and growth, with a particular focus on areas with lower historical fishing mortality; and 2) conduct simulations focused on the Indian Ocean stock to explore the potential of stock assessments and auxiliary analyses to estimate M and other model parameters using data from tagging studies.

Introduction

Natural mortality (M) is a very influential parameter in fish stock assessments but is also difficult to estimate either within integrated stock assessment models or independently (Maunder et al., 2023). Various sources of information have been used to support independent M estimates in different species, including the age structure of the population, the maximum observed age, tagging data, and inferences from related species. Two of the main components to estimate are the mean value of M , and its possible variation among population subgroups (e.g., sexes and age classes). In 2021, an analysis of potential approaches for modelling natural mortality was initiated for yellowfin tuna (Hoyle, 2021a), which led to publication on natural mortality estimates for all stocks of yellowfin tuna (Hoyle et al., 2023). After comments by the IOTC Working Party on Tropical Tunas, additional analysis has been requested. The aim of this work is to compare approaches for defining appropriate levels of M for inclusion in stock assessments of Indian Ocean bigeye (Fu, 2019) and yellowfin (Fu et al., 2021) tuna, including:

1. Investigate the influence of alternative M assumptions on management advice, by running IO YFT and BET assessments with different M ogives and mean values.
2. Recommend default assumptions for use in IOTC stock assessments.
3. Recommend research to improve estimates of the most influential aspects of M .

Initially, the data, methods, and natural mortality ogives used for bigeye stock assessments by all tuna RFMOs were explored via a literature review.

Many aspects of the determination of natural mortality at age were considered, including

- methods for estimating the target level of M ,
- methods for determining relative M at age,
- methods for combining the target M with M at age,
- whether or not M should vary by sex; and
- whether or not M should vary between oceans.

Data and approaches by tuna RFMO

Oldest fish (otoliths)

IOTC

The oldest fish in the most recent study was 14.7 years from ageing of 108 otoliths (Farley et al., 2021). However, an earlier study that included 809 otoliths from Western Australia and 393 from the Indonesian region observed a maximum age of 16 years (Farley et al., 2006). Fish in the latter study were sampled randomly from longline fisheries, but otoliths were selected with some stratification based on area of capture and length, with the aim of estimating ages of fish from a representative sample of the size range of bigeye caught in each fishery.

WCPFC

The oldest fish aged using otoliths in the WCPO was approximately 15 years (Ducharme-Barth et al., 2020) from 1172 otoliths (Farley et al., 2020).

IATTC

NA (daily ageing only).

ICCAT

The oldest fish aged was 17 years old (Andrews et al., 2020). This was considered low since the number of fish aged was just over 200, and samples came from an already heavily-depleted stock (ICCAT, 2021b).

Time at liberty

WCPFC

The longest period at liberty for a recaptured bigeye tuna tagged in the WCPO was approximately 14 years, for a fish 1-2 years old at release (SPC unpublished data) (Ducharme-Barth et al., 2020; Langley et al., 2008), indicating an age of 15-16 years.

IOTC

The longest time at liberty was eight to nine years, corresponding to an age of eleven to twelve years (Langley, 2016).

IATTC

The longest time at liberty was eight years (Aires-da-Silva et al., 2015).

ICCAT

Longest time at liberty in 2019 was five to six years (ICCAT, 2019).

Estimation approaches for natural mortality

IOTC

In 2006, Hillary and Mosqueira (2006) developed a bigeye tuna assessment with the integrated assessment package CASAL (Bull et al., 2003), using natural mortality at ages 0 to 6+ of 1, 0.6, 0.3, 0.4, 0.4, 0.4, 0.4. They ran two sensitivity trials, the first with M at age 0 increased to 1.2, and the second with juvenile natural mortality of 0.6 for ages 0 and 1. They noted that changing M at age 0 affected B_0 , but had little effect on depletion, selectivity, or fits to the data. Also in 2006, Shono et al. (2006) developed a preliminary assessment of bigeye tuna using Stock Synthesis 2 (Methot, 2005). Natural mortality at ages 0 to 6+ was 0.8, 0.8, 0.4, 0.4, 0.4, 0.4, 0.4. They ran sensitivity analyses with a different trend for juveniles: 1, 0.8, 0.6, 0.4, 0.4, 0.4, 0.4; with the same ogive as the CASAL model: 1, 0.6, 0.3, 0.4, 0.4, 0.4, 0.4; and adding senescence: 1, 0.6, 0.3, 0.4, 0.4, 0.4, 0.6. However, it is unclear from the report how these changes affected results.

In 2009 Shono et al. (2009) updated this assessment using the original M at age ogive. Nishida and Rademeyer (2009) ran an ASPM assessment using M of 0.8 for ages 0 and 1, and 0.4 for ages 2 to 9+.

In 2010, Kolody et al. (2010) introduced Stock Synthesis 3 (Methot and Wetzel, 2013), with the baseline M vector derived from Shono et al. (2009). They trialed two additional ogives with M for all ages raised or lowered by 20%. Higher M led to estimates that the stock was in better condition. Attempts to estimate M were not considered credible, since the model consistently referred lower M for younger ages, and also because the analysts considered that, given the structure of the model, the data are unlikely to be informative about M . Nishida and Rademeyer (2010) updated their model from 2009 but did not change the M at age.

In 2011 Zhu et al. (2011) ran a tuned VPA assessment with the same M ogive as Shono et al. (2009).

In 2013, bigeye assessments were run using ASAP (Zhu et al., 2013), ASPM (Nishida and Iwasaki, 2013), and SS3 Langley (Langley et al., 2013). All 3 used the same Shono et al. (2009) M ogives as in previous versions, but Langley et al. (2013) introduced a curve with a lower natural mortality for adult age classes (0.0625 per quarter).

The 2016 bigeye stock assessment using SS3 Langley (2016) explored the implications of these two alternatives natural mortality ogives, particularly with reference to adult M , and considered the lower level more plausible since it allowed the model to fit better to the tag data. There were a considerable number of tag recaptures after 7–8 years at liberty, indicating that proportion of these fish reach an age of 8–10 years; 8 tags were recovered after 10 years at liberty and a few tags were recovered in 2015, corresponding to an age at recovery of 11–12 years.

The 2019 stock assessment for Indian Ocean bigeye tuna (Fu, 2019) used two alternative levels of natural mortality, following Langley (2016). The higher level of natural mortality was considered comparable with IATTC and WCPFC approaches, with relatively high M for the younger age classes and M of about 0.1 per quarter for adults. The lower level of natural mortality was proposed based on a Lorenzen curve analysis, along with lower natural mortality for the adult age classes (0.0625 per quarter). This was seen as comparable to the level of natural mortality assumed for Atlantic bigeye tuna in the 2015 ICCAT stock assessment (ICCAT, 2016). An inverse relationship between M and age/size (high M for juveniles and low M for adults) is well established (Lorenzen, 1996; Lorenzen, 2000; Lorenzen, 2005; Lorenzen et al., 2022) and corresponds well with some of the biological factors contributing to the variability of natural mortality of tuna (Fonteneau and Pallares, 2004).

Natural mortality in the 2019 assessment is provided in Figure 1, along with ogives currently used by each of the other 3 tuna RFMOs that assess stocks of bigeye tuna.

IATTC

As described in Xu et al. (2020). “Age-specific vectors of natural mortality (M) are assumed for bigeye in the EPO. This assessment uses sex-specific models and natural mortality schedules are provided for each sex (Figure 3.2 in Aires-da-Silva and Maunder, 2010). M at age 0 is assumed to be 0.25 for both sexes, and M is assumed to decrease to 0.1 at 5 quarters of age. As in previous assessments, it is assumed that female M increases after the fish mature. These age-specific vectors of M are based on fitting to the estimates of age-specific proportions of females, maturity at age, and M of Hampton (2000).” In fact, most of the decrease to 0.1 occurs by 4 quarters, when M is equal to 0.101087.

The effects of alternate juvenile M on the outcomes of the bigeye stock assessment have been evaluated by running the model with 5 alternative M ogives for males and females (IATTC Staff, 2008).

WCPFC

M -at-age was calculated using an approach applied to other tunas in the WCPO and EPO (Harley and Maunder, 2003; Hoyle, 2008; Hoyle and Nicol, 2008). The generally increasing proportion of males observed in the catch with increasing size was assumed in these analyses to be due to an increase in the natural mortality of females, associated with sexual maturity and the onset of reproduction. Values of M -at-age were initially calculated at-length, back-transformed to age using the growth curve, and input to the MFCL assessment model as fixed values.

Meta-analysis using different life-history based M estimators was conducted more recently (Vincent et al., 2020) to provide a range of plausible natural mortality values for the assessment (Ducharme-Barth et al., 2020). These included the lower 95% confidence interval (0.109; M -low), the mean (0.127; M -mid) and the upper 95% confidence interval (0.146; M -hi). As a sensitivity analysis these values were applied to the age-specific deviates used in the diagnostic case.

ICCAT

In the 2021 ICCAT bigeye assessment, natural mortality ogives were calculated by applying the Then et al. (2015) estimator to a maximum observed age of 17 years (Andrews et al., 2020), and scaling the ogive so that natural mortality was a Lorenzen function of weight at age (Lorenzen, 1996) (ICCAT, 2021a). The method is described more fully later in the section ‘Methods for combining the target M with M at age’. Additional ogives were based on alternative maximum ages of 20 and 25, because the aged fish were sampled from a heavily fished stock (ICCAT, 2021b).

Further considerations

Methods for estimating the target level of M

The oldest fish observed in a population (A_{max}) can be used to infer a target level of natural mortality, based on meta-analyses of databases of A_{max} and M estimates (Hamel and Cope, 2022; Hoenig, 1983; Then et al., 2015). Then et al (2015) updated the Hoenig (1983) estimator by greatly increasing the size of the database. Hamel and Cope (2022) used the Then et al (2015) database but identified an improvement to the statistical methods that materially changed the resulting predictions. We recommend that the Hamel and Cope (2022) (HC) approach should be used rather than the Then et al (2015) method. An earlier version of this WP recommended both methods, but publication of the Hamel and Cope (2022) paper after peer review allows us to focus on the new method.

Methods for determining relative M at age

It is increasingly well established that natural mortality is inversely proportional to length, formalized as the generalized length-inverse mortality paradigm (GLIM, Lorenzen, 2022; Lorenzen et al., 2022), although deviations from the length-inverse pattern may occur in older ages due to senescence and in early juveniles due to density-dependence. There is also little evidence for a step change in natural mortality between juveniles and adults (Lorenzen et al., 2022). We therefore recommend using this approach in preference to the more complicated method discussed at WPTT 2021 and implemented in Stock Synthesis (Hoyle, 2021b; Hoyle et al., 2023; Maunder and Aires-da-Silva, 2012; Methot et al., 2021).

Although senescence is a feature of semelparous fishes, it is not commonly observed in iteroparous fish species (Beverton and Holt, 1959; Craig, 1985). Senescence may be negligible in populations with indeterminate growth and the potential for increasing fecundity with age (Purchase et al., 2022). Bigeye and other tuna species appear to fall into this category and continue to grow throughout life (Farley et al., 2021; Farley et al., 2020; Waterhouse et al., 2022), although growth slows with time, and there is a possibility of growth cessation (Maunder et al., 2018).

Methods for combining the target M with M at age

Lorenzen et al. (2022) found that predictions of constant M based on Then et al. (2015)'s growth-based empirical predictor (which is distinct from the predictor based on A_{max}) were approximately equal to size-dependent M values at around the center of the adult size range. They argued that "this supports the established practice of scaling the 'Lorenzen M ' so that its average over the adult size or age groups equals empirical estimates of constant M (SEDAR (Southeast Data, Assessment and Reviews), 2018)." However, the evidence for applying the growth-based empirical predictor to adult age classes does not necessarily transfer to other empirical predictors. The approach for applying them will depend on the information that was used to estimate them.

Applications of Lorenzen M at age for Atlantic bigeye (e.g., ICCAT, 2021a; ICCAT, 2021b; Schirripa, 2016) have combined the two components (target M and Lorenzen curve), largely using the approach adopted by the Southeast Data, Assessment and Review (SEDAR) process, as documented by Porch (2011). It should be noted that this approach differs somewhat from the recommendation of Lorenzen et al. (2022) in that the average is applied across fully exploited age classes rather than across adult age classes.

Porch (2011) describes the approach to rescale the Lorenzen curve so that the average mortality rate matches a target value over the relevant life history period. "This is typically accomplished in three steps: 1) the Lorenzen curve is converted to a function of age by use of a growth equation, 2) the target value of M is determined external to the assessment model, and 3) the Lorenzen curve is rescaled such that $M_t = M_{target} \frac{n\lambda_t}{\sum_{t=t_c}^{t_{max}} \lambda_t}$, where t is age, λ_t is the age-converted Lorenzen curve, t_c is the first fully exploited age class, t_{max} is the oldest age class, and n is the number of exploited age classes. [In other words, M_{target} is multiplied by $\lambda_t / \text{mean}(\lambda)$, across the range of fully exploited age classes.] The results of this rescaling approach are sensitive to the value of t_c when it falls within the age range where growth is rapid."

The Atlantic bigeye approach is a little more complicated. First, length at age t_c is calculated, based on a von Bertalanffy growth curve, as $len_{t_c} = L_{\infty}(1 - e^{-K(t_c - t_0)})$. Next, an adjusted mortality at unit length, M_1 , is calculated as:

$$M_1 = \frac{(t_{max} - t_c)L_\infty KM_{target}}{\log\left(\frac{len_{t_c}}{len_{t_c} + L_\infty(e^{K(t_{max}-t_c)} - 1)}\right)} \quad (1)$$

Lengths at age are calculated based on the midpoint of the age class, using the equation:

$$len_{t+0.5} = L_\infty(1 - e^{-K(t-t_0+0.5)}) \quad (2)$$

M is then estimated at each age class t as $M_t = M_1/len_{t+0.5}$, based on the assumption that M is inversely proportional to length (Lorenzen et al., 2022). A slightly more accurate formulation of M at age integrates across the growth curve for the period inc between ages t and $t+1$, given the units of K .

$$M_t = -\log\left(\frac{len_t}{len_t + L_\infty(e^{K.inc} - 1)}\right) \cdot \frac{M_1}{L_\infty K} \quad (3)$$

Should M vary by sex?

As previously discussed (Hoyle, 2021b; Hoyle et al., 2023), M has been assumed in the past to vary by sex due to the predominance of males at large sizes, as seen in all species of *Thunnus*. However, ageing using annuli has provided considerable evidence that males grow to larger sizes than females in all *Thunnus* species. This contributes some of the difference in sex ratio at length and may be the only reason for the difference. Although differences in M by sex remain possible, they are likely considerably smaller than previously supposed, if they occur at all. Lacking reliable estimates of length at age by sex for bigeye tuna in the Indian Ocean, we do not have a basis for estimating sex differences in M .

Should M vary between oceans?

Natural mortality is affected by both intrinsic and extrinsic factors. Extrinsic factors include abiotic challenges, predation pressure, competition, and exposure to pathogens, all which may vary to some degree between stocks and through time. Intrinsic factors, which originate within the organism, are likely to be similar across stocks and through time. They include physiological resilience, costs of reproduction, anti-predator responses, competitive ability, and disease resistance/immunity (see Lorenzen, 2022, for more information). Inherently intrinsic effects such as senescence and sex-dependent mortality are unlikely to vary between stocks, so the observation of the oldest fish in one stock suggests that senescence is unlikely at younger ages in any stock.

Since extrinsic factors that affect natural mortality, and hence the rate of natural mortality, may vary between locations, including between oceans (e.g., Strøm et al., 2019), M from one stock will be an uncertain estimator for another stock. However, estimates of natural mortality based on A_{max} are affected by the history of fishing mortality experienced by the stock. Inferences from the Then et al (2015) database should ideally be applied to relatively unfished stocks. Estimates of A_{max} from a heavily fished stock (such as Indian Ocean bigeye tuna) may therefore be biased low (and M biased high). Estimates can also be affected by the amount and quality of age sampling, such that estimates of A_{max} for areas with limited sampling (such as the Indian Ocean data used by Farley et al. (2021)), may similarly be biased low. In such cases, inferring M from the A_{max} of a conspecific in another location that is less heavily exploited and better sampled is a reasonable approach for determining M .

What if all stocks are heavily exploited?

Bigeye tunas are assessed to be currently quite heavily exploited in all oceans, which tends to truncate the time series. Ageing using annuli is a recent development, so there are (to my knowledge) no samples from earlier periods when exploitation was light. Maximum ages are likely to reflect the effects on age structure of total mortality rather than natural mortality alone. However, maximum ages will be increased by spatial heterogeneity in fishing pressure on the stock, so it is not appropriate to estimate M by assuming that the A_{max} empirical method estimates Z , and that $M=Z-F$. Ideally, maximum age should be obtained by sampling longline catches as broadly as possible, and potentially by longline surveys in areas with a history of low fishing effort.

Uncertainty

There are various sources of uncertainty in M estimates:

- The symmetrical error distribution in the relationship between A_{max} and M . This can be characterized.
- Uncertainty about which age classes to include in the reference period. Negative bias from too many young age classes, or positive bias from old age classes.
- Positive bias due to low sample sizes and limited sampling distribution (IO: $n=108$, AO: $n\sim 200$).
- Positive bias due to exploitation of the stocks.

Analysis

The input files for the 2019 bigeye stock assessment were modified to run with the four alternative versions of natural mortality. No other parameters were modified.

In addition, the input files for the 2021 yellowfin stock assessment were modified to run with two alternative versions of Lorenzen natural mortality, based on the oldest fish aged locally (10.7 years) and globally (18 years) (Hoyle et al., 2023).

Results

Proposed values of M for IOTC

Alternative values of bigeye target M (i.e., the natural mortality predicted by the empirical method) were calculated based on maximum observed ages of 16 years in the Indian Ocean and 17 years in the Atlantic Ocean.

Maximum age	Then et al 2015	Hamel and Cope (2022)
IO=16	0.386	0.338
AO=17	0.365	0.317

The target M for bigeye tuna was distributed across age classes using the Lorenzen curve and the Farley et al. (2021) von Bertalanffy growth curve, with the target M equal to the average M of age classes 1 to 15 (Figure 2 and Table 1). The ogive Then17 differed slightly from the corresponding ICCAT ogive due to the differences between the growth curves and because the ICCAT ogive calculated mean size for fish of age t based on expected size at age $t + 0.5$, replacing len_t with $len_{t+0.5}$ in equation (3). We avoided doing this since the adjustment is already accounted for within equation (3), which integrates across ages t to $t + inc$, where inc is equal to 1.

The inverse relationship of natural mortality with length had a particularly large impact on M for young bigeye tuna. All resulting estimates of natural mortality were considerably higher than even the high 2019 ogive for fish up to about 1 years of age.

The bigeye stock assessment models run with the two alternative versions of natural mortality fitted the data about as well as the 2019 model (Figure 3), with a slight improvement in likelihood for the model with the lower natural mortality (HC 17) and slightly worse likelihood for the model with the higher natural mortality (HC 16).

All bigeye models with Lorenzen M tended to have lower spawning biomass time series estimates than the base model (Figure 4), but the spawning biomass ratio $SSB / SSB0$ trends were almost identical (Figure 5). The time series of total biomass started lower for the Lorenzen M models, but all models ended up at similar levels (Figure 6). The F ratio time series indicated slightly lower F / F_{msy} , particularly at the end of the time series, for the Lorenzen M models compared to the 2019 assessment (Figure 7). Impacts on recruitment were much larger, with highest average recruitment estimated for model Then 14.7 which had the highest natural mortality (Figure 8).

For yellowfin tuna, the combined-sex M estimate in the 2021 stock assessment included the effects of increased M for females (Figure 9). The Lorenzen ogives based on the global maximum observed age had considerably lower M for all ages, while the ogive based on local maximum observed age had lower M for fish older than about 3 years.

The yellowfin stock assessment models run with the two alternative versions of natural mortality fitted the data worse than the 2021 assessment model (Figure 10), particularly the model based on global maximum age, with much of the difference coming from fits to the length frequency data.

The yellowfin models with Lorenzen M tended to have higher spawning biomass time series estimates than the 2021 assessment model (Figure 11), although the model based on local maximum age was almost identical. The spawning biomass ratio $SSB / SSB0$ trends were also similar for the model based on local maximum age, but the model based on global maximum age declined more than the 2021 assessment (Figure 12). The time series of total biomass started higher for the Lorenzen M models, and both models ended up at lower levels (Figure 13). The F ratio time series indicated higher F / F_{msy} levels, particularly at the end of the time series, for the Lorenzen M models compared to the 2021 assessment (Figure 14). Impacts on recruitment followed a similar pattern, with lowest mean recruitment estimated for the model based on global maximum age, which had the lowest natural mortality (Figure 15).

Discussion

The natural mortality estimates provided here are based on the oldest fish observed, following the Hamel and Cope (2022) analysis of the Then et al (2015) database of M estimates. It is reasonable to apply such an empirically based estimator to the same range of age classes as were used to develop the estimator. Then et al. (2015) state that “Most of the M estimates were derived from age-based catch curve analyses (79%), 5% from length-based catch curves, 8% from tagging, and 2% from the regression of total mortality rate vs. effort (or variants).” We can therefore infer that the 215 M estimates in the Then et al. (2015) database were based on fully exploited age classes.

However, it is unclear whether all the exploited age classes contribute equally to the mostly age-invariant M estimates included in the database. For example, tagging-based estimators generally include fewer of the older, rarer age classes, if fish are tagged in proportion to abundance. In some cases, such as tuna tagging on pole and line vessels, tagged fish are almost exclusively young and

small (Fonteneau and Hallier, 2015; Leroy et al., 2013). Tagging-based estimators may therefore estimate M to be higher, since younger fish are expected to have higher M . Catch curve analyses, on the other hand, potentially include all ages up to t_{max} , usually assuming asymptotic selectivity at age of the fishery providing the samples. They will omit some younger age classes that are not fully selected, with full selection judged by the catch curve's linearity on the log scale. They may also give equal statistical weight to each age class, rather than weighting in proportion to numbers. Catch curves may therefore tend to estimate lower M than tag-based estimators.

Changing to Lorenzen M and reducing mean natural mortality had less impact on the bigeye assessment outcomes than might be expected, given the large differences in M -at-age apparent in Figure 2. However, the largest differences in natural mortality occur for very small fish before or in the early stages of recruitment to the fishery. Changing M for unexploited age classes mostly serves to scale recruitment since it does not affect the relative numbers at age exploited age classes. The low level of variation between model runs may also reflect the impact of the tags in the assessment model, since they tend to constrain the estimates of fishing mortality in the fisheries that capture the tags. Since catch in those fisheries is assumed known, this also constrains the biomass vulnerable to those fisheries. The fisheries taking the most tags are fisheries 5 (R1 free school purse seine - south), 9 (R1 associated purse seine -south), and 15 (R1 associated purse seine - north). Hence, the biomass of all models tends to be similar in the period of tag recovery (pseudo-years 315-355 for the bigeye assessment, and 238-260 for the yellowfin assessment), particularly for purse-seine vulnerable biomass in R1.

The yellowfin assessment also has very similar total biomass in all models during the tagging period, but more variation among models in initial biomass and SSB/SSB0, given the larger changes in natural mortality of adult fish.

Assessment likelihoods for both species tended to favor models with higher M estimates, with the greatest contributions to the relative likelihoods coming from fits to the length frequency data. However, this should not be taken to imply that higher M estimates should be preferred. M estimates from stock assessments are sensitive to model misspecification (Maunder et al., 2023). Many aspects of these assessments are poorly understood and likely to be misspecified, with particular concern about tag mixing (Kolody and Hoyle, 2015) and assumptions about selectivity, growth, and spatial size patterns (Hoyle et al., 2021). At this stage it is better to infer M from external analyses (i.e., the analyses reported in this paper) rather than to give weight to the relative fits of different M estimates.

Given these issues, the default recommendation for Indian Ocean stock assessments is to apply 2 alternative ogives based on the approach applied in this paper: a combination of the oldest observed fish, and the distribution of M at age proposed by Lorenzen et al. (2022). There is insufficient evidence to support an age of senescence for either bigeye or yellowfin tuna. Similarly, there is currently insufficient evidence to apply sex dependent M for either species.

Better understanding is needed of the potential to estimate M and other model parameters either within the bigeye and yellowfin stock assessments (Fu, 2019; Fu et al., 2021), or in auxiliary analyses of tagging data (e.g., Eveson et al., 2012). One of the main problems for these methods is the assumptions about the movements and mixing of tagged and untagged fish (Hoening et al., 1998). The current project to explore methods for spatial stock assessment, partly based around an operating model for Indian Ocean yellowfin tuna (Dunn et al., 2020) is not directly focused on this issue, but has demonstrated the sensitivity of model results to spatial configuration and assumptions. There is potential for further work using a combination of simulation using the existing

operating model, and analysis of the IOTC tagging database, to identify the best ways to extract reliable information from the tagging data. This appears to be warranted given the large investment in collecting the tagging data, and the uncertainty about whether current modelling approaches are appropriate.

Expanded age sampling is also recommended for bigeye and yellowfin tuna across all areas of the Indian Ocean, to obtain more reliable and broadly-based information about both maximum ages and growth curves, both of which contribute to Lorenzen estimates of M at age. It would be particularly useful to obtain samples from areas in which fishing mortality is lower, and from longline fisheries, to obtain older fish. However, fisheries that target smaller fish must also be sampled to avoid bias in the growth curve.

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Tables

Table 1: Four alternative ogives of quarterly natural mortality for bigeye tuna.

Age	Length	Then15	Then17	Hamel15	Hamel17
0	24	0.480	0.420	0.422	0.365
0.25	35	0.354	0.310	0.312	0.270
0.5	45	0.286	0.250	0.251	0.217
0.75	54	0.242	0.212	0.213	0.184
1	62	0.212	0.186	0.187	0.162
1.25	70	0.191	0.167	0.168	0.145
1.5	77	0.174	0.152	0.153	0.132
1.75	84	0.161	0.141	0.142	0.123
2	90	0.151	0.132	0.133	0.115
2.25	96	0.143	0.125	0.125	0.108
2.5	101	0.136	0.119	0.119	0.103
2.75	106	0.130	0.113	0.114	0.099
3	110	0.125	0.109	0.110	0.095
3.25	115	0.120	0.105	0.106	0.091
3.5	118	0.117	0.102	0.102	0.089
3.75	122	0.113	0.099	0.100	0.086
4	125	0.110	0.097	0.097	0.084
4.25	128	0.108	0.094	0.095	0.082
4.5	131	0.106	0.093	0.093	0.080
4.75	134	0.104	0.091	0.091	0.079
5	136	0.102	0.089	0.090	0.078
5.25	139	0.100	0.088	0.088	0.076
5.5	141	0.099	0.087	0.087	0.075
5.75	143	0.098	0.085	0.086	0.074
6	144	0.096	0.084	0.085	0.073
6.25	146	0.095	0.084	0.084	0.073
6.5	148	0.094	0.083	0.083	0.072
6.75	149	0.094	0.082	0.082	0.071
7	150	0.093	0.081	0.082	0.071
7.25	152	0.092	0.081	0.081	0.070
7.5	153	0.091	0.080	0.080	0.070
7.75	154	0.091	0.080	0.080	0.069
8	155	0.090	0.079	0.079	0.069
8.25	156	0.090	0.079	0.079	0.068
8.5	156	0.089	0.078	0.079	0.068
8.75	157	0.089	0.078	0.078	0.068
9	158	0.089	0.078	0.078	0.067
9.25	159	0.088	0.077	0.078	0.067
9.5	159	0.088	0.077	0.077	0.067
9.75	160	0.088	0.077	0.077	0.067
10	160	0.087	0.076	0.077	0.066

Figures

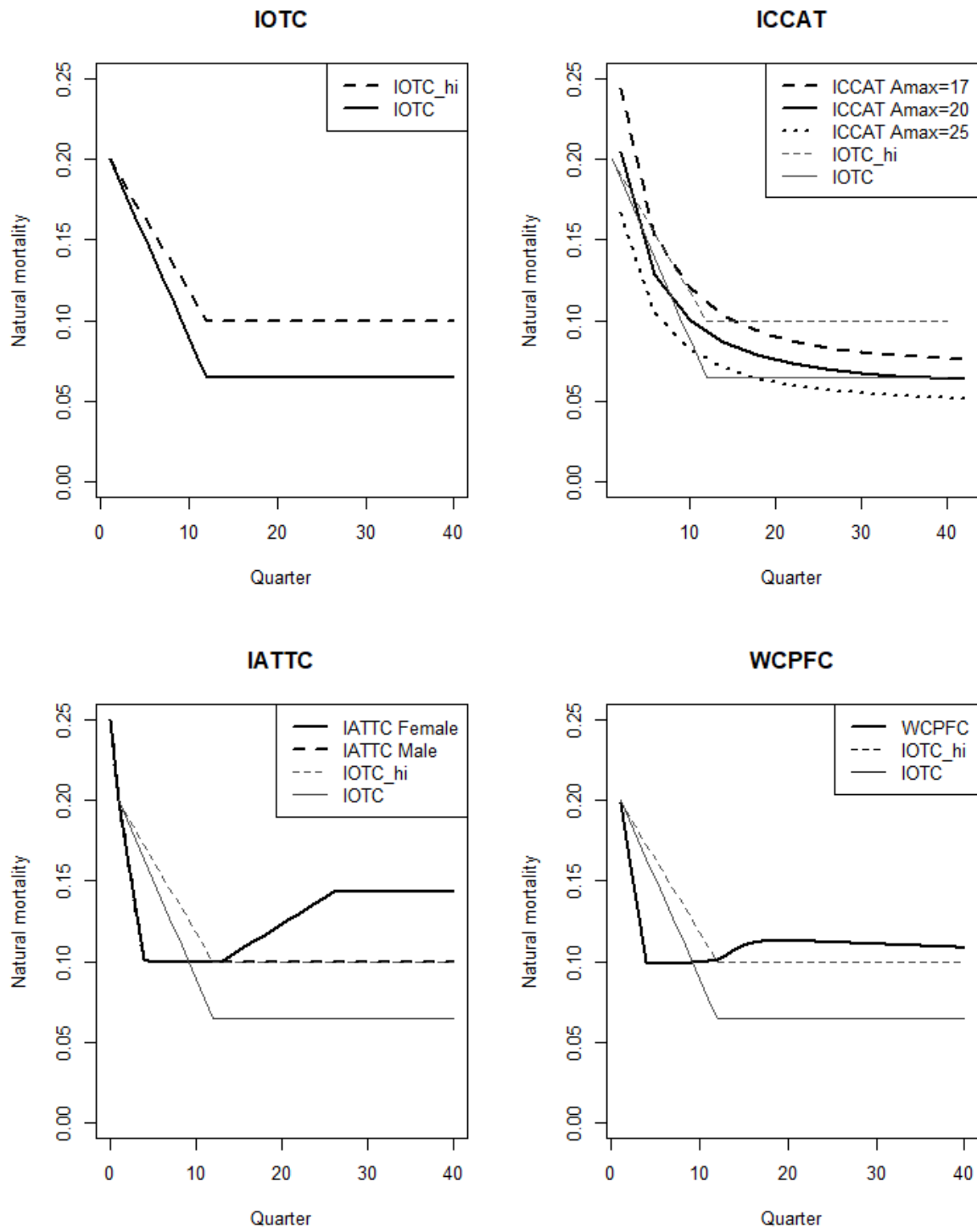


Figure 1: Quarterly natural mortality at age ogives for bigeye tuna used by each of the four tRFMOs that conduct bigeye stock assessments. The IOTC ogives are included in all subplots for comparison with the ogives used by the other tRFMOs.

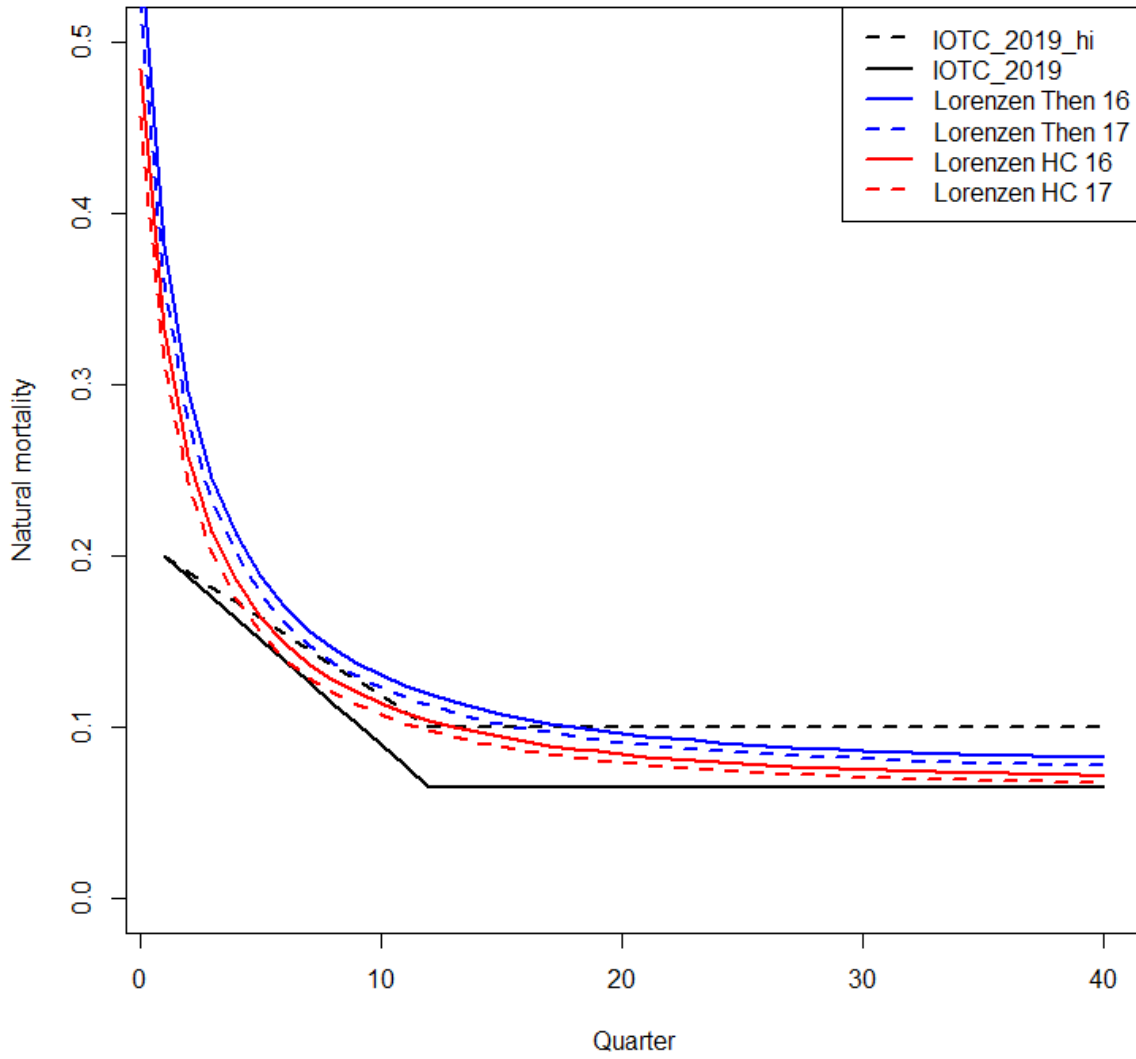


Figure 2: Natural mortality ogives used in the 2019 Indian Ocean bigeye tuna assessment, and the Lorenzen ogives proposed for the 2022 assessment.

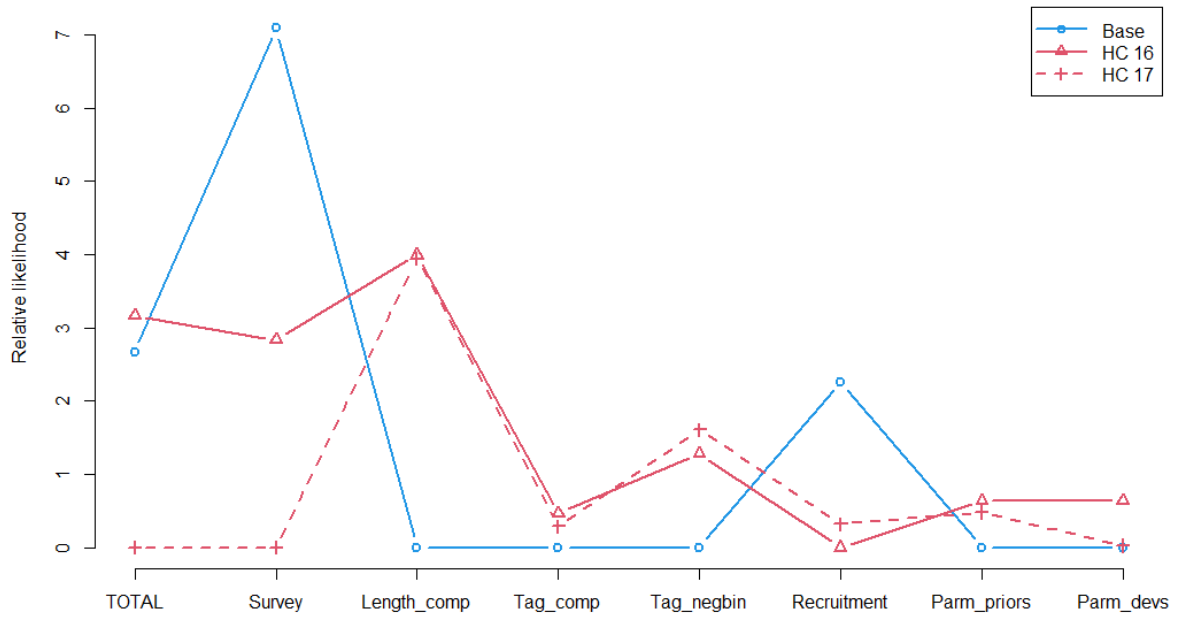


Figure 3: Relative total log likelihoods and the main likelihood components for each of the three models for bigeye tuna.

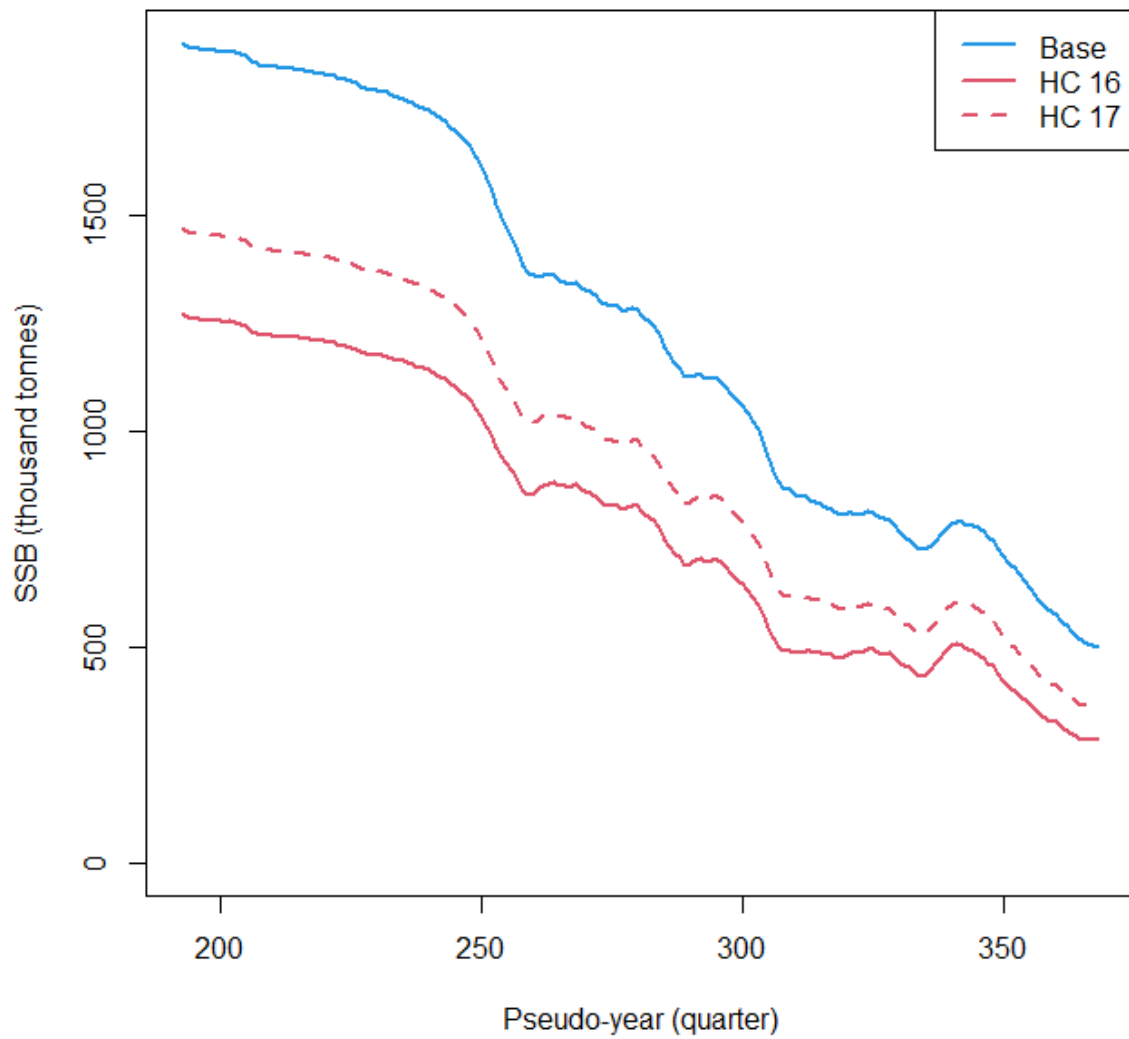


Figure 4: Estimated spawning biomass time series for each of the three models for bigeye tuna.

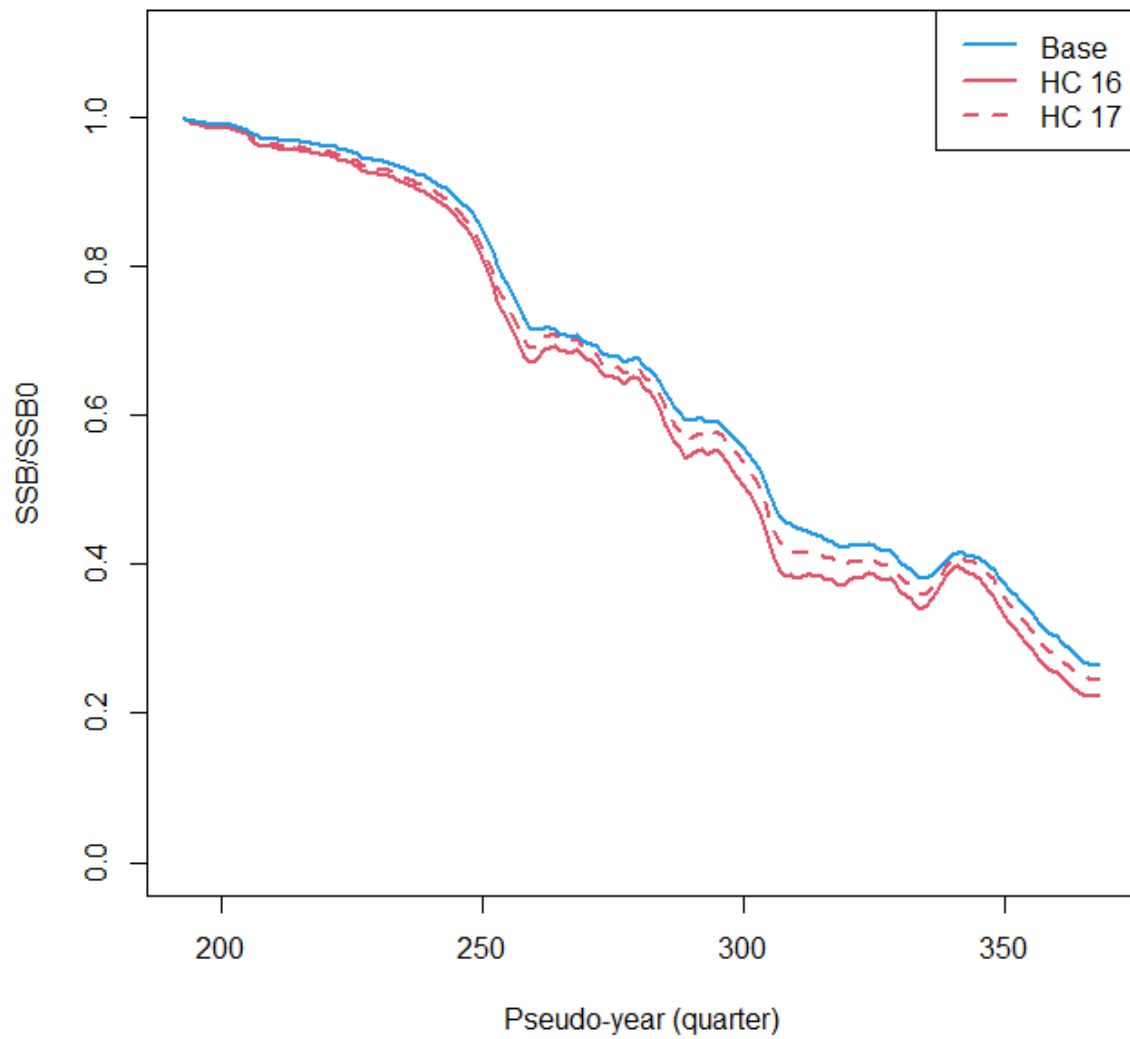


Figure 5: Estimated time series of the ratio SSB / SSB_0 for each of the three models for bigeye tuna.

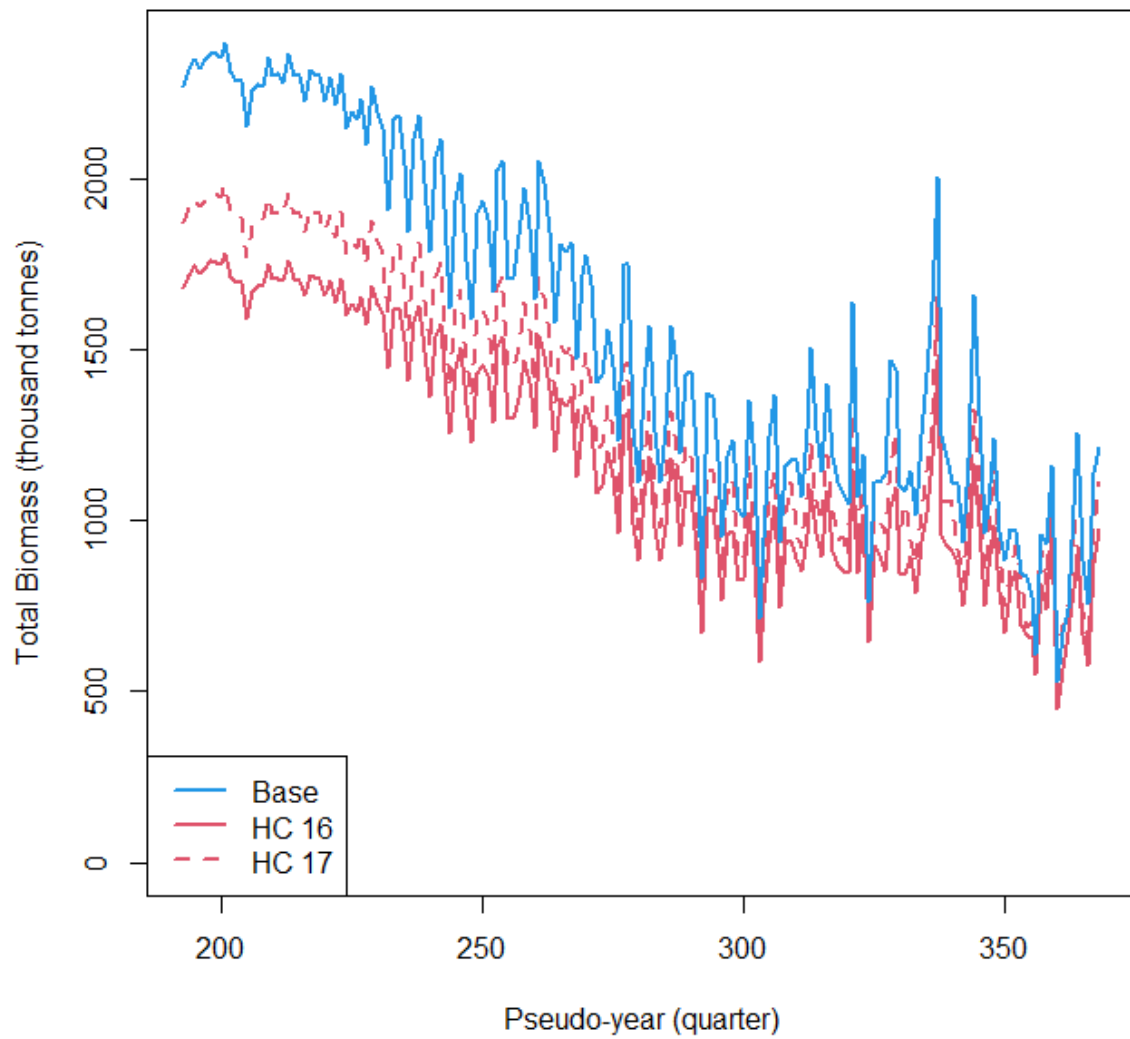


Figure 6: Time series of total biomass estimated for each of the three models for bigeye tuna.

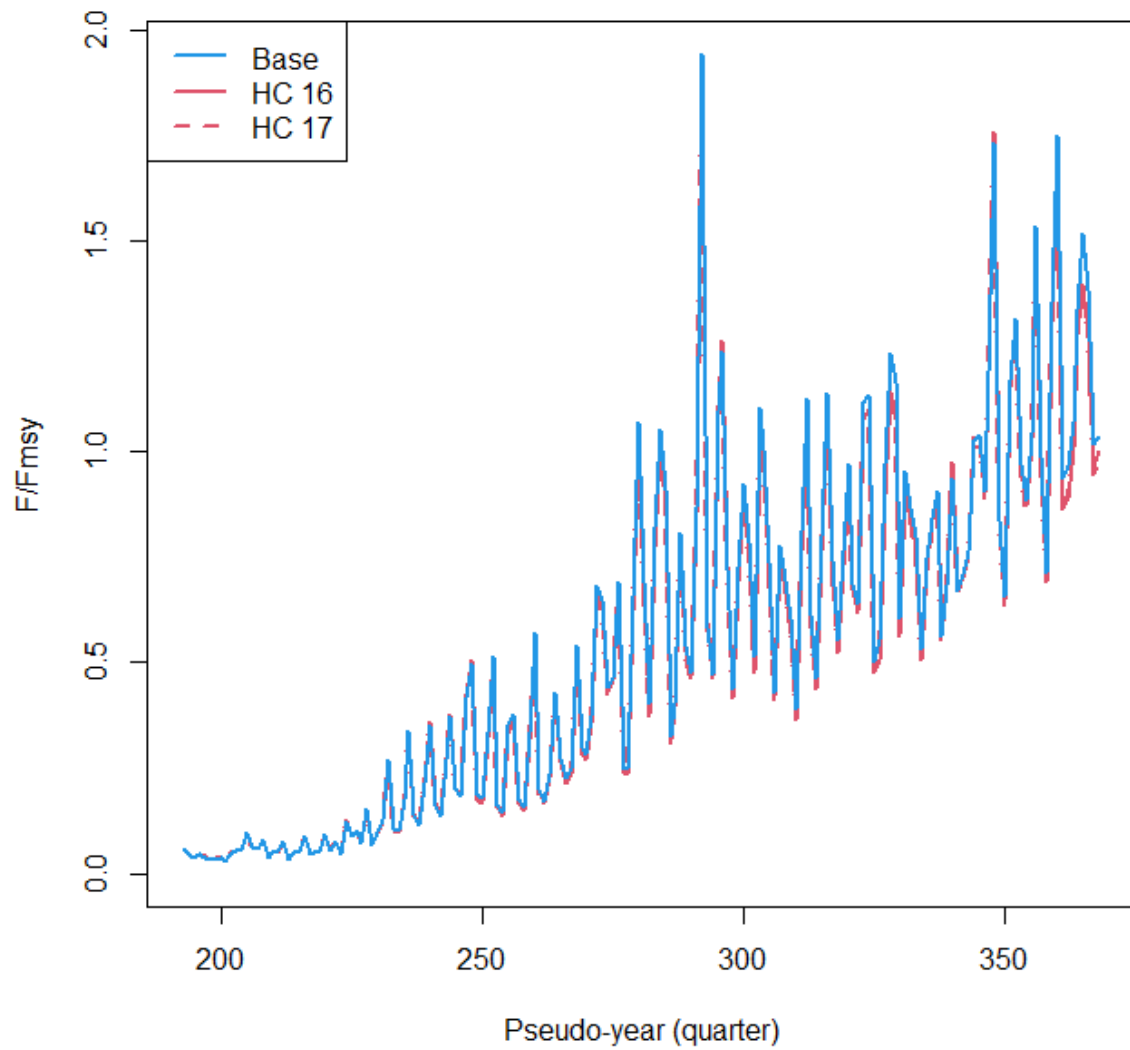


Figure 7: Estimated time series of the ratio F / F_{msy} for each of the three models for bigeye tuna.

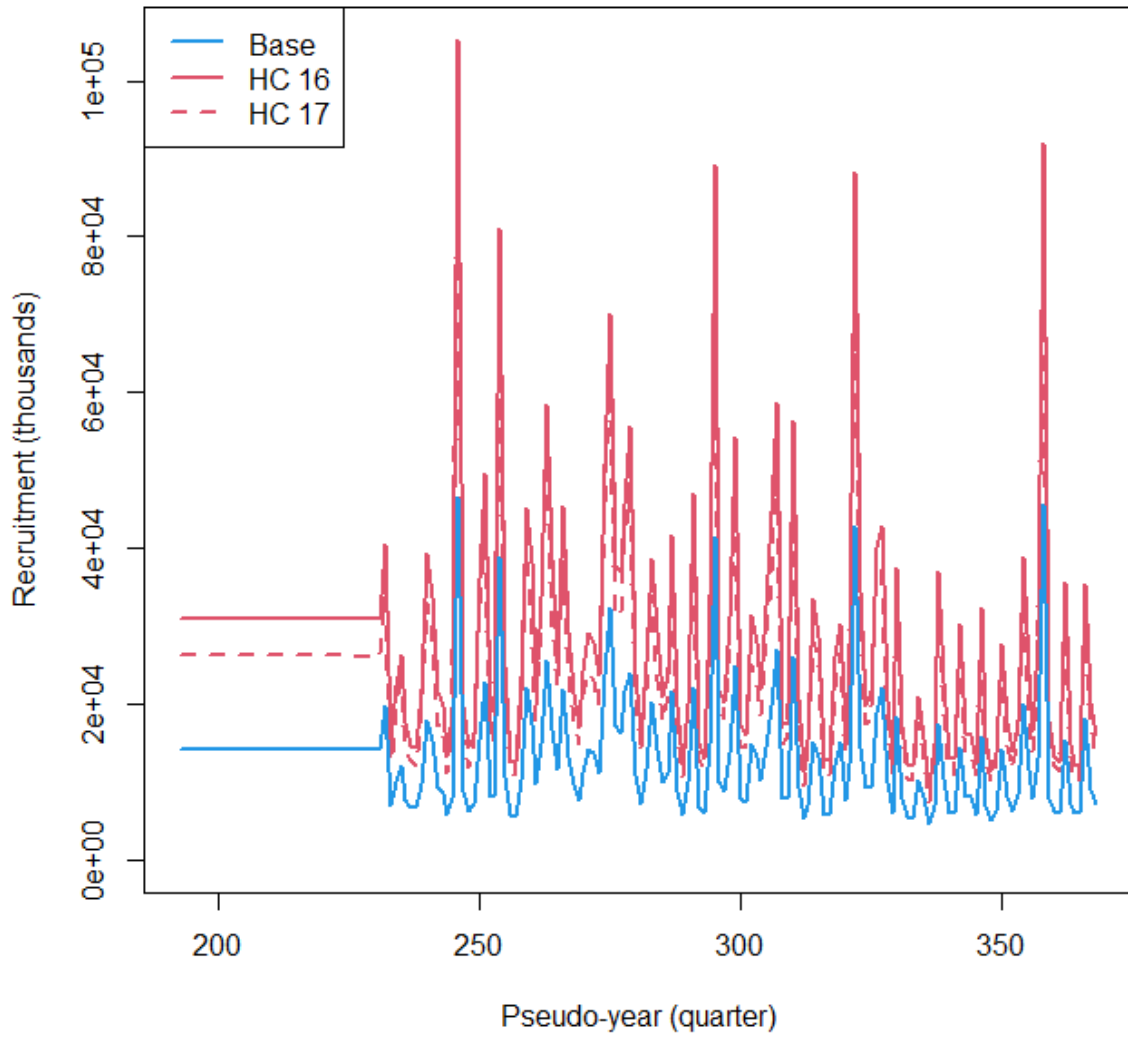


Figure 8: Estimated time series of quarterly recruitments for each of the three models for bigeye tuna.

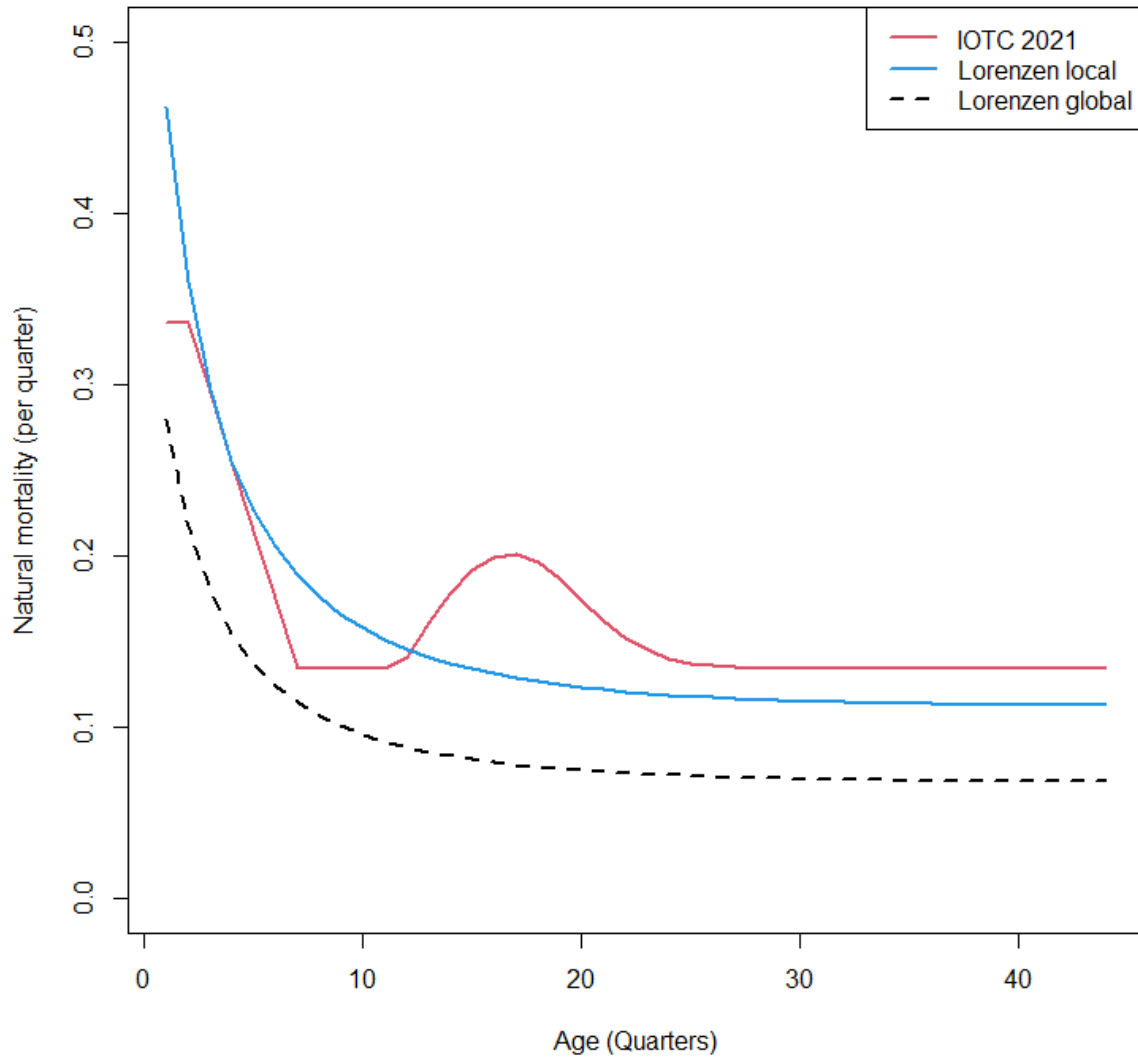


Figure 9: Natural mortality (quarterly) ogives used in the 2021 Indian Ocean yellowfin tuna assessment, and the Lorenzen ogives based on the IO yellowfin growth curve and maximum ages of 10.7 (local) and 18 (global).

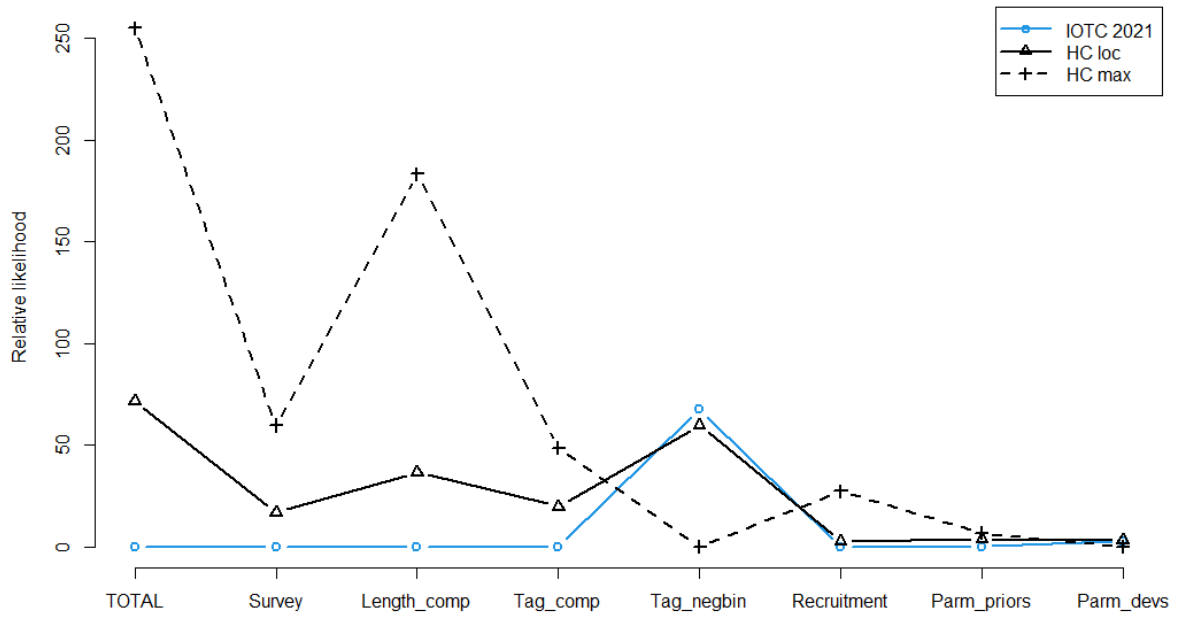


Figure 10: Relative total log likelihoods and the main likelihood components for each of the 3 models for yellowfin tuna.

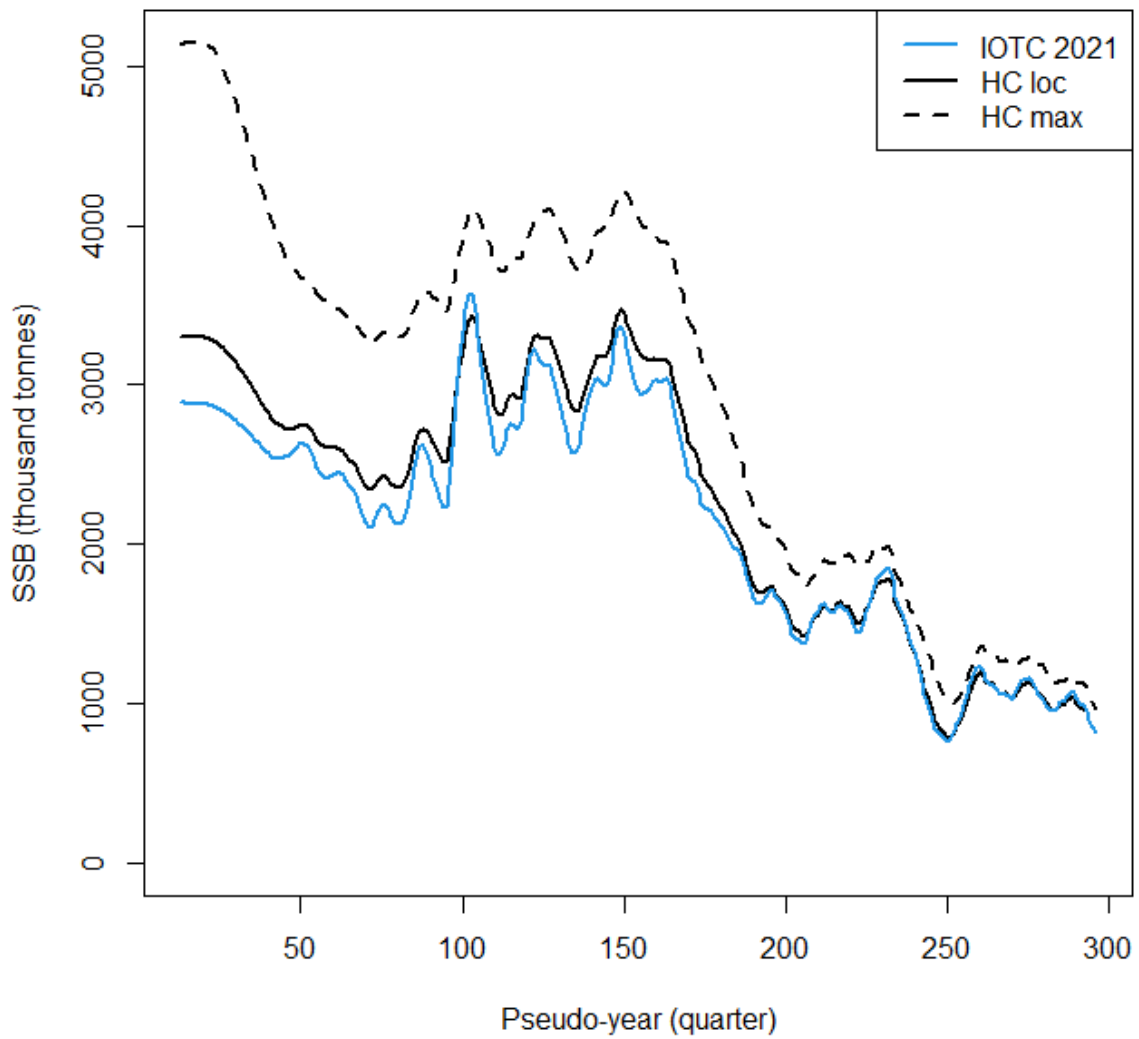


Figure 11: Estimated spawning biomass time series for each of the three models for yellowfin tuna.

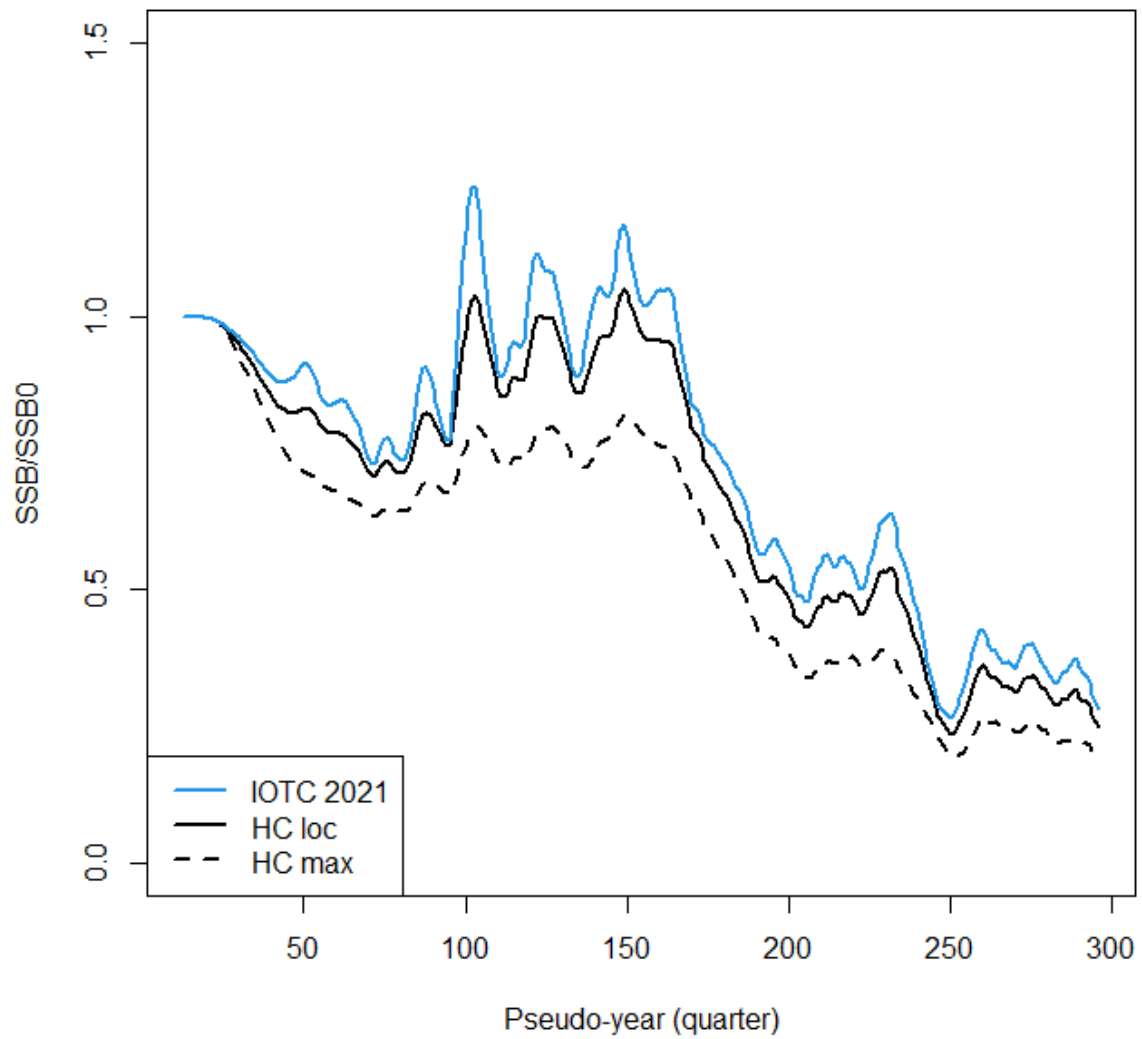


Figure 12: Estimated time series of the ratio $SSB / SSB0$ for each of the three models for yellowfin tuna.

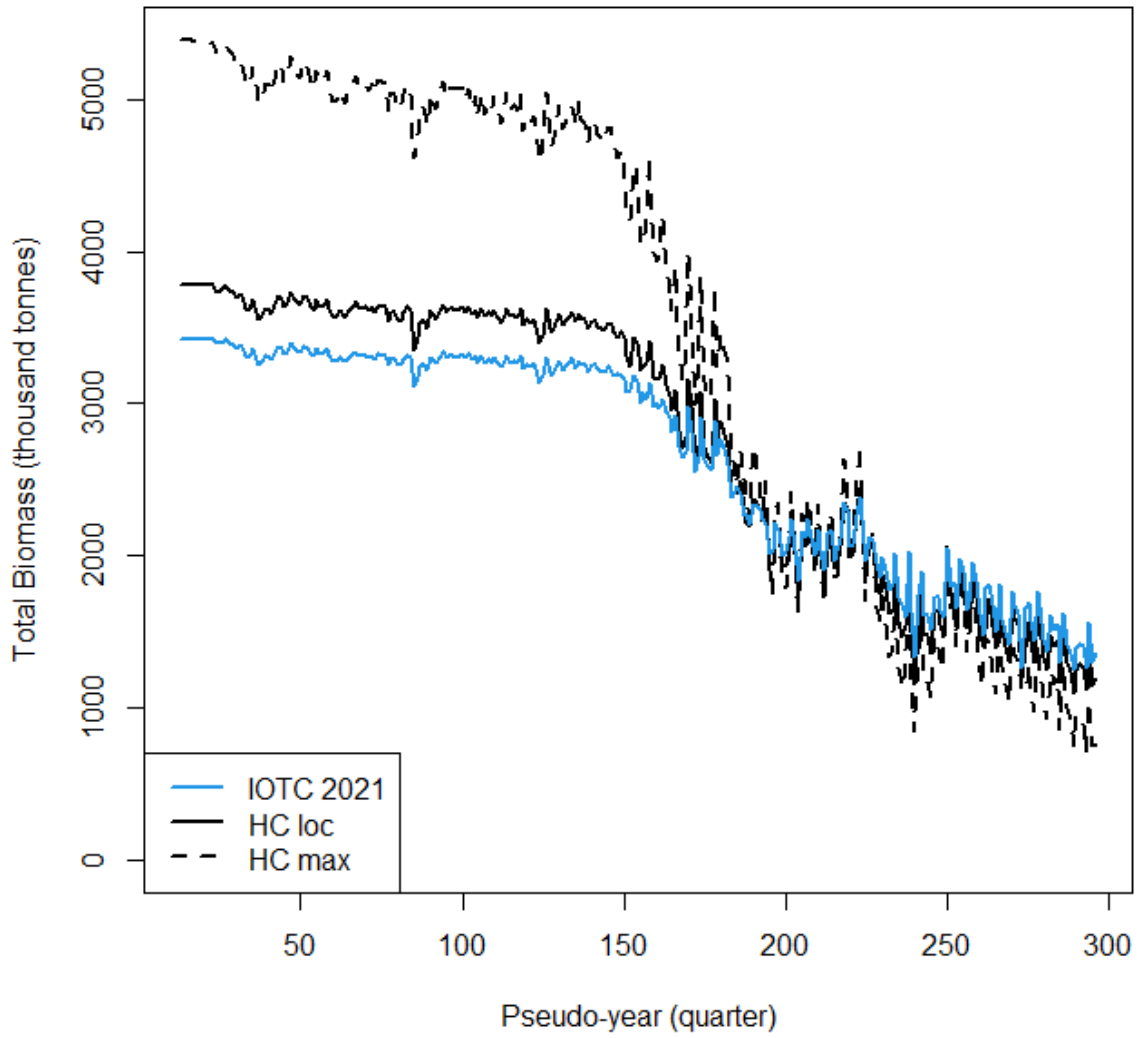


Figure 13: Time series of total biomass estimated for each of the three models for yellowfin tuna.

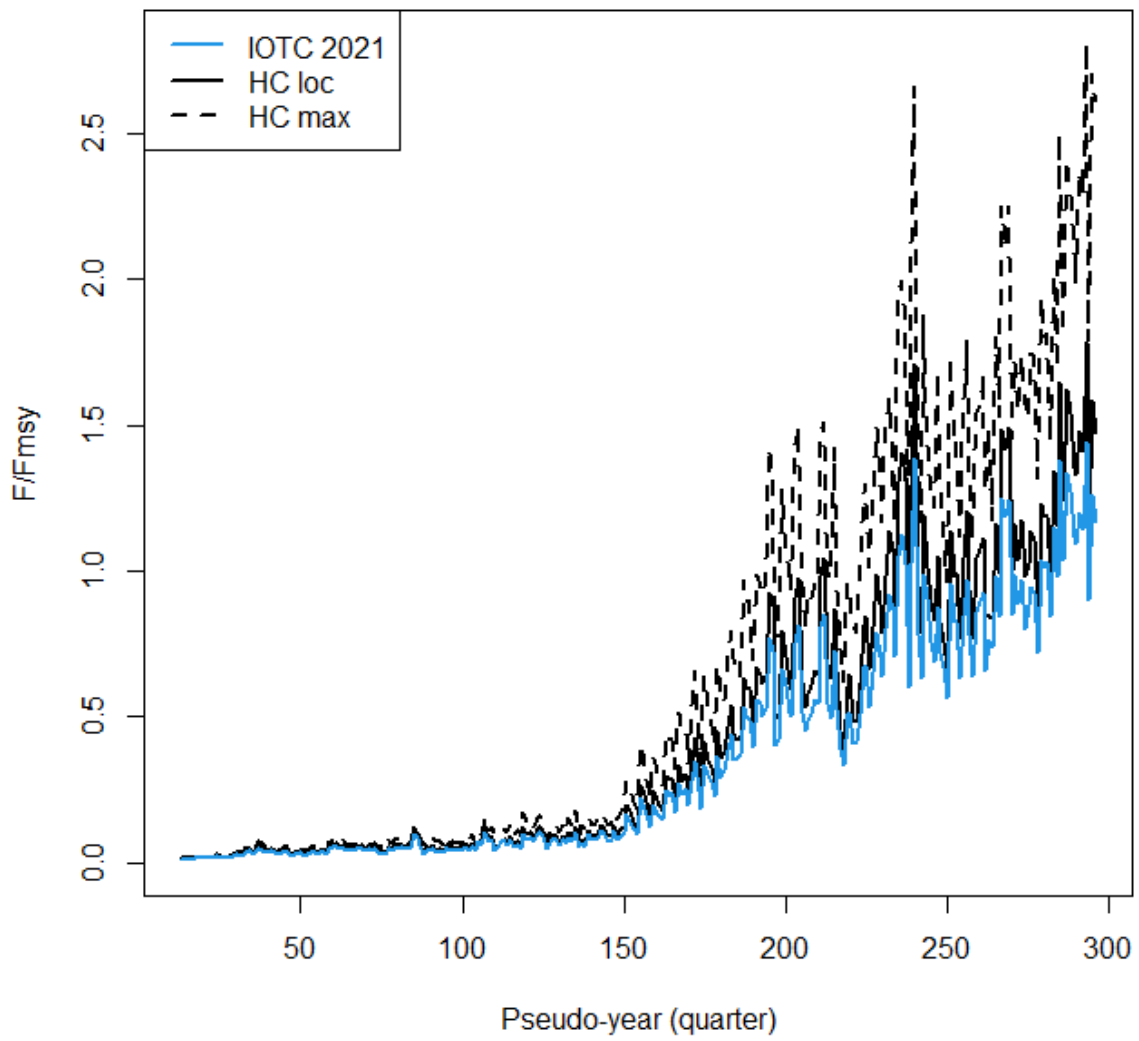


Figure 14: Estimated time series of the ratio F / F_{msy} for each of the three models for yellowfin tuna.

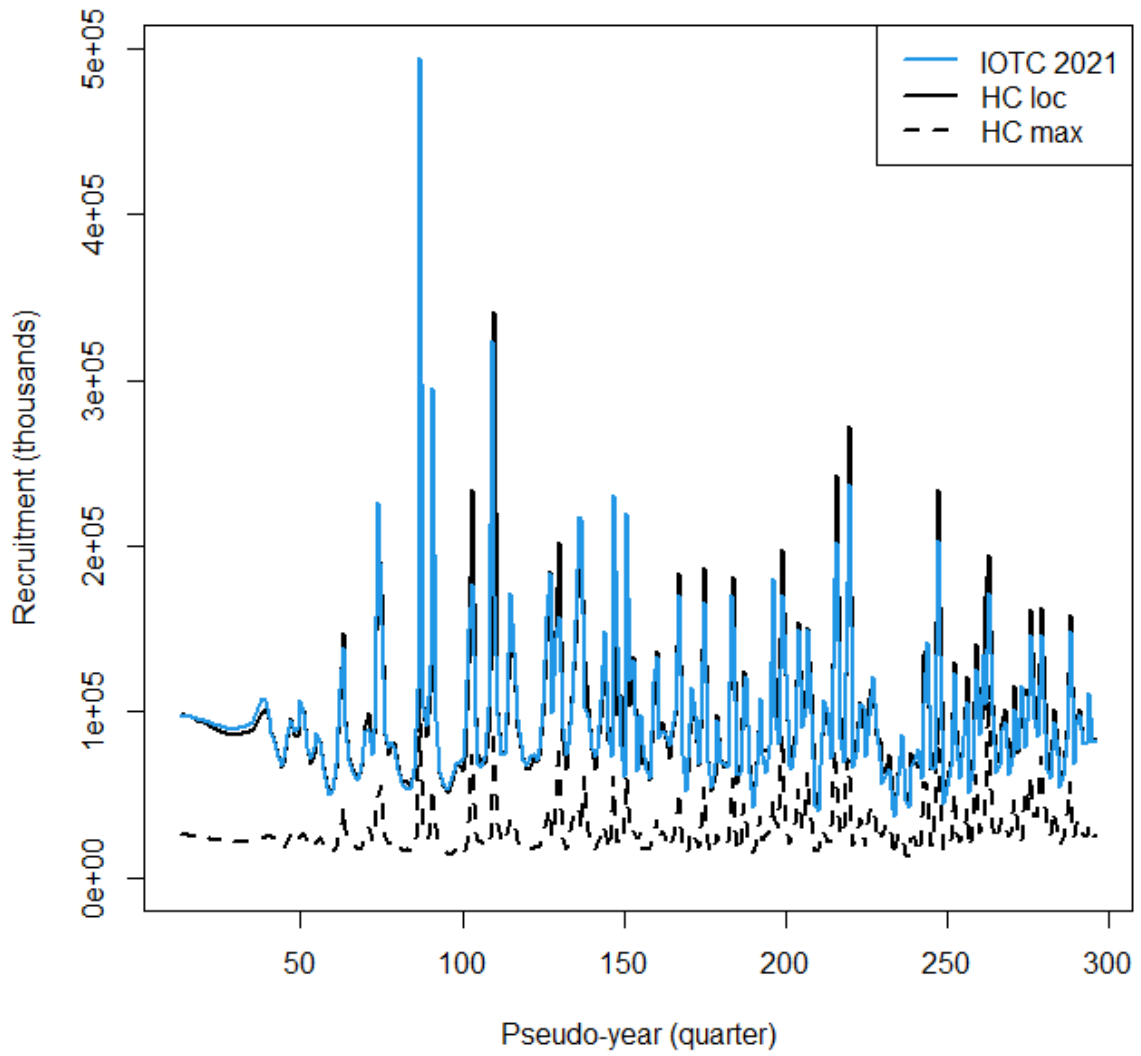


Figure 15: Estimated time series of quarterly recruitments for each of the three models for yellowfin tuna.